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Afrotropical Asilidae (Diptera) 26. Ethological observations, and a possible ecological classification based on habitats

by

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ABSTRACT

Biological information relating to Afrotropical Asilidae is briefly reviewed. An ecological classification of genera, based on field-observed surveillance positions adopted by adults, is proposed. Six major categories, each usually subdivided into secondary categories, are employed viz. 1. Ground (a. Beaches, b. River banks, c. General); 2. Stones (a. Riparian, b. General); 3. Rocks; 4. Grass (a. Within, b. Tips); 5. Shrubs & bushes (a. Within, b. Tips); 6. Trees (a. Within, b. Tips). Based on ovipositor structure, asilid genera are further analysed in terms of their oviposition behaviour within the identified ecological categories. Three oviposition strategies are identified viz. 1. Random egg-dropping; 2. Oviposition in sand or soil; 3. Oviposition on or in vegetation. Finally, based on an analysis of 1608 accumulated prey records, the importance of prey choice within the suggested ecological classification is briefly discussed. An important point arising from this work, is that field-experienced taxonomists are best placed to promote the much-needed ecological work still required to be undertaken on the vast majority of insect taxa.

INTRODUCTION

The Asilidae constitute one of the most important families of predatory insects. They prey on other insects and spiders in almost every terrestrial habitat in the Afrotropical Region; from tropical rain-forests to deserts, from coastal beaches to montane grasslands. Although adults are easily recognised by most entomologists, there is still much to be learned about the vast majority of species. The bulk of previous research effort has been invested in taxonomic studies. Biological and ecological information is largely limited to brief, somewhat isolated comments, buried in taxonomic publications and in unpublished dissertations. The purpose of this paper is to provide an overview of existing biological information about Afrotropical Asilidae, and to document some of the knowledge gained over the 17 years I have dedicated to the study of this large family. Although most of my published work is taxonomic, much time has been spent observing Asilidae in the field. Most of these observations have never been published. While collecting expeditions to Namibia (3), Malaŵi (2), Kenya (1) and Ivory Coast (1) have been undertaken, most of my experience has been accumulated in South Africa, particularly the Cape and Natal provinces. This means that my knowledge of asilid groups uncommonly found in southern Africa remains limited to what has been learnt during the few trips made to the countries listed above. This deficiency is not serious as southern Africa is probably the most diversely rich subregion within the afrotropics, and the species encountered further north appear to share the same general characteristics as observed in southern Africa.

Although there is an apparent paucity of biological and ecological information on Afrotropical Asilidae, a reasonably sound general understanding of these flies has been gained using information available to me in four forms: i. The limited literature. ii. Field observations. iii. Morphology of museum specimens. iv. Accumulated prey records. Using these sources it is possible to gain an understanding of both the adult feeding and oviposition behaviours of most groups within the family.

GENERAL MATERIALS AND METHODS

Specimens used in this study are mostly housed in the Natal Museum. Data relating to prey preferences are contained in a Natal Museum database. To save space, authors of generic names are given only in the tables, and not in the text; dates of publication of taxa are excluded as these may be obtained by consulting the Afrotropical Diptera Catalogue (Oldroyd 1980) and the more recent publications cited in this paper.

REVIEW OF BIOLOGICAL INFORMATION ON AFROTROPICAL ASILIDAE

Although much useful information regarding Asilidae in general may be gleaned from literature dealing with non-Afrotropical species, the following bibliographic review has been limited to work on Afrotropical taxa. This review may be incomplete as brief notes contained in papers which are otherwise purely taxonomic in content may have been missed. Because of the vastness of the region covered, the many taxonomic inadequacies which still exist, and the general paucity of biological information, much of the analysis has had to be resolved at a generic level. For convenience genera have been listed alphabetically.

General biology

Papers dedicated to aspects of the biology of Afrotropical asilid species are rare and comprise the general comments on *Hyperechia marshalli* published by Engel & Cuthbertson (1934) and the more recent work of Londt & Harris (1987) on *Neolophonotus dichaetus* and Londt (1991) on *Damalis femoralis*.

Ovipositor morphology

As ovipositor morphology is important in gaining an understanding of the oviposition behaviour of largely unstudied asilids, the following list of references to good published illustrations is useful: *Afromelittodes* – Oldroyd 1974; *Alcimus* – Oldroyd 1974; *Ammodaimon* – Londt 1985*c*; *Astochia* – Londt 1982*b*; *Bana* – Londt 1992*b*; *Clinopogon* – Londt 1979*b*; *Congomochtherus* – Oldroyd 1974, Londt & Tsacas 1987; *Damalis* – Oldroyd (as *Xenomyza*) 1974; *Daspletis* – Oldroyd 1974; *Dysclytus* – Oldroyd 1974, Londt 1979*a*; *Empodiodes* – Londt 1992*a*; *Gibbasilus* – Londt 1986*a*; *Habropogon* – Londt 1981*a*; *Heligmonevra* – Oldroyd 1974; *Hermannomyia* – Londt 1981*a*; *Afroholopogon* (as *Heteropogon*) Oldroyd 1974; *Hippomachus* – Londt 1983*b*; *Hynirhynchus* – Londt 1992*a*; *Hyperechia* – Oldroyd 1974; *Laphystotes* – Oldroyd 1974; *Lasiocnemus* – Oldroyd 1974; *Laxenecera* – Oldroyd 1974; *Lycostommyia* – Londt 1992*a*; *Microstylum* – Oldroyd 1974; *Neolophonotus* – Oldroyd 1974, Londt 1985*d*, Londt & Harris 1987; *Neomochtherus* – Oldroyd 1974; *Ommatius* – Oldroyd 1974; *Pilophoneus* – Londt 1988*b*; *Pycnomerinx* – Londt 1990*c*; *Rhabdogaster* – Oldroyd 1974; *Rhipidocephala* –

Oldroyd 1974; *Scylaticus* – Oldroyd 1974; *Smeryngolaphria* – Londt 1989*b*; *Sporadothrix* – Oldroyd 1974; *Stichopogon* – Oldroyd 1974, Londt 1979*b*; *Stiphrolamyra* – Londt 1983*a*; *Synolcus* – Oldroyd 1974, Londt 1980*a* 1990*b*; *Teratopomyia* – Oldroyd (as *Teratopus*) 1974; *Trichardis* – Oldroyd 1974.

Oviposition behaviour

Positively recorded or suggested sites of oviposition are provided for species in the following genera: *Alcimus* – Cuthbertson 1934; *Congomochtherus* – Londt & Tsacas 1987; *Damalis* – Londt 1991; *Dysclytus* – Londt 1979*a*; *Neolophonotus* – Londt & Harris 1987; *Pegesimallus* – Londt 1980*b*; *Synolcus* – Londt 1980*a*.

Egg morphology

Details of egg morphology are provided for species in the following genera: *Damalis* – Londt 1991; *Neolophonotus* – Londt & Harris 1987; *Smeryngolaphria* – Londt 1989*b*.

Incubation

Information regarding the incubation of eggs is limited to: *Damalis* – Londt 1991; *Neolophonotus* – Londt & Harris 1987.

Larval morphology

Information on larval morphology exists for a few genera: *Alcimus* – Engel & Cuthbertson 1934; *Damalis* – Londt 1991; *Hyperechia* – Engel 1930; *Neolophonotus* – Engel & Cuthbertson 1939, Londt & Harris 1987.

Larval behaviour

Although all asilid larvae are believed to be predatory, notes on the larval behaviour of Afrotropical species are limited to three genera: *Alcimus* – Cuthbertson 1933, Engel & Cuthbertson 1934; *Hyperechia* – Engel 1930; *Neolophonotus* – Engel & Cuthbertson 1939, Londt & Harris 1987.

Pupal morphology

Information is available for the following genera: *Alcimus* – Engel & Cuthbertson 1934; *Gibbasilus* – Londt 1986*a*; *Hyperechia* – Engel 1930, Engel & Cuthbertson 1934; *Neolophonotus* – Engel & Cuthbertson 1939; *Proagonistes* – Engel 1932; *Promachus* – Engel & Cuthbertson 1939. No specific information exists regarding pupation or eclosion.

Adult ecological data

General comments regarding where adults may be found, exist for species in many genera: *Alcimus* – Engel & Cuthbertson 1934; *Ammodaimon* – Londt 1985*c*; *Anypodetus* – Engel & Cuthbertson 1934; *Astochia* – Londt 1982*a*; *Clinopogon* – Londt 1979*b*; *Congomochtherus* – Londt & Tsacas 1987; *Damalis* – Cuthbertson (as *Lophurodamalis*) 1938, Londt 1989*a* 1991; *Dasophrys* – Londt 1981*b*; *Dysclytus* – Londt 1979*a*; *Euscelidia* – Engel & Cuthbertson 1934; *Goneccalypsis* – Londt 1982*a*; *Gonioscelis* – Engel & Cuthbertson 1934 1939; *Hippomachus* – Londt 1983*b* 1985*a*; *Hoplistomerus* – Cuthbertson 1933; *Hypenetes* – Engel & Cuthbertson 1939, Londt 1985*b*; *Lasiocnemus* – Engel & Cuthbertson 1934; *Laxenecera* – Engel & Cuthbertson 1934; *Microstylum* – Cuthbertson 1933, Engel & Cuthbertson 1938; *Nannolaphria* – Londt 1977; *Neolophonotus* – Cuthbertson 1938, Londt 1985*d* 1986*b*, Londt & Harris 1987; *Oligopogon* – Engel & Cuthbertson 1939; *Ommatius* –

Cuthbertson 1933 1934 1938; *Oratostylum* – Londt 1985*a*; *Pegesimallus* – Cuthbertson (as *Neolaparus*) 1938, Engel & Cuthbertson (as *Neolaparus*) 1939, Londt 1980*b*; *Philodicus* – Londt 1978; *Proagonistes* – Engel 1932; *Pycnomerinx* – Londt 1990*c*; *Scylaticus* – Londt 1992*c*; *Stichopogon* – Cuthbertson 1938, Engel & Cuthbertson 1939, Londt 1979*b*; *Stiphrolamyra* – Londt 1983*a*; *Synolcus* – Londt 1980*a* 1990*b*; *Trichardis* – Engel & Cuthbertson 1934 1939.

Adult feeding behaviour

General information on adult feeding is available for the following genera: *Damalis* – Londt 1991; *Microstylum* – Cuthbertson 1938, Engel & Cuthbertson 1938; *Pegesimallus* – Londt 1980*b*. The role of hypertrophied wings in Nemopteridae (Neuroptera) on predation by four genera of South African asilids was covered by Picker, Leon & Londt (1991 1992).

Prey records

General references dealing with Afrotropical asilid prey selection include Hobby (1935 – a survey of predator/prey records from Zimbabwe) and Londt (1987*a* 1990*a* – abstracts of congress papers), while predation on honey bees has been dealt with by Bromley (1949) and Londt (1993*a*). Details contained in these works are not included in the survey below. Other prey records have been given for species within the following genera: *Alcimus* – Cuthbertson 1933 1934, Engel & Cuthbertson 1934, Cuthbertson 1938; *Anypodetus* – Engel & Cuthbertson 1934; *Bana* – Londt 1992*b*; *Damalis* – Cuthbertson (as *Lophurodamalis*) 1938, Londt 1989*a* 1991; *Daspletis* – Londt 1983*c* 1985*a*; *Dysclytus* – Londt 1979*a*; *Gonioscelis* – Engel & Cuthbertson 1934 1939, Cuthbertson 1938; *Hoplistomerus* – Cuthbertson 1933; *Hypenetes* – Engel & Cuthbertson 1939, Londt 1985*b*; *Lamyra* – Cuthbertson 1938; *Laxenecera* – Engel & Cuthbertson 1934, Cuthbertson 1938; *Microstylum* – Cuthbertson 1933 1938, Engel & Cuthbertson 1934; *Nannolaphria* – Londt 1977; *Neolophonotus* – Engel & Cuthbertson (as *Lophopeltis*) 1934 1939, Cuthbertson 1938 (as *Lophopeltis*), Londt 1985*a* 1986*b* 1987*b* 1988*a*, Londt & Harris 1987; *Oligopogon* – Engel & Cuthbertson 1939; *Ommatius* – Cuthbertson 1933 1934 1938; *Pegesimallus* – Engel & Cuthbertson (as *Neolaparus*) 1934, Cuthbertson (as *Neolaparus*) 1938, Londt 1980*b*; *Philodicus* – Cuthbertson 1938, Londt 1978; *Promachus* – Cuthbertson 1934 1938, Engel & Cuthbertson 1939; *Scylaticus* – Engel & Cuthbertson 1934, Londt 1992*c*; *Stichopogon* – Cuthbertson 1938, Engel & Cuthbertson 1939, Londt 1979*b*; *Stiphrolamyra* – Londt 1983*a*; *Trichardis* – Engel & Cuthbertson 1939.

Mating

Isolated notes on mating behaviour are available for the following genera: *Astochia* – Londt 1982*b*; *Damalis* – Cuthbertson 1938 (as *Lophurodamalis*), Londt 1991; *Dysclytus* – Londt 1979*a*.

ECOLOGICAL CLASSIFICATION

No attempt has hitherto been made to classify Afrotropical Asilidae with respect to the habitats they normally occupy. Although there are a number of publications dealing with the habitat preferences of non-Afrotropical species, few authors have attempted to provide an overview of even a small regional fauna. The following two exceptions are worthy of mention.

Lehr (1979), using his considerable experience of the Palaearctic fauna, developed interesting thoughts on a system of ecological classification in which he identified six 'trophic complexes', using the prey-capturing strategies of the adult Asilidae involved (Fig. 1). With the additional aid of an unpublished translation of part of Lehr's original article, sent to me by the author, the following English summary of his classification may be presented.

Trophic complex	*Asilid feeding behaviour*
Geophils	Hunt from surface of bald earth
Herpetobions	Hunt from the surface of the earth but in the grass thicket
Chortobions	Hunt inside the grass thicket
Epiphytobions	Hunt above the grass surface
Epiphytogeobions	Hunt both the surface of the earth and from the grass
Tamnobions	Hunt from the trees

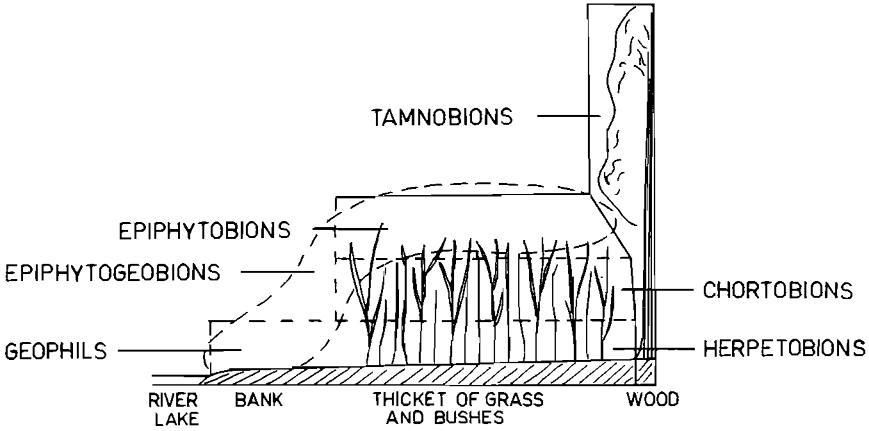

Fig. 1. The 'life forms' of Asilidae as suggested by Lehr (1979).

The other attempt to group Asilidae in ecological categories on the basis of their usual perching positions, was included in a published account of the taxonomy and biology of Mesoamerican Asilidae (Fisher & Hespenheide 1992). In their table, these authors provided a classification of asilids related to 'microhabitat and perch' as follows:

Forest Understorey
    Twigs, tip
    Twigs, crosswise [ie. body at right-angle to twig]
    Twigs, parallel [ie. body parallel to twig]
    Leaf surfaces
    Ground

Forest streams
    Twig tips
    Leaf surfaces
Treefall gaps – Forest edge

Fisher & Hespenheide superimposed on this arrangement information relating to whether the asilids perched in shade or sun (ie. 'Sun flies' and 'Shade flies') and recorded both the size and weight of flies, and included an assessment of relative abundance.

Both these attempts to provide an ecological classification of asilids suffer from inherent inadequacies, the most serious of which is their inability to adequately encompass other faunas. While Lehr's arrangement appears to be more easily adapted to the Afrotropical fauna, it does not make provision for a number of categories identified through my own experience and would, therefore, require further refinement.

Based largely on field observations of the surveillance (= resting = perching = hunting) positions adopted by adult individuals, the following ecological classification has been developed (see also Fig. 2).

1. *Ground* (includes expanses of soil, sand and compact earth as well as more restricted ground surfaces such as roadways, paths or exposed places between grass tussocks etc.).
    a. *Beaches* (a highly specific subcategory encompassing marine beaches and associated, sometimes vegetated, dunes. Also included are the sandy edges of saline lagoons and estuaries close to the sea).
    b. *River banks* (a subdivision including the sandy, often damp, banks of streams and rivers).
    c. *General* (ie. all 'ground' situations not found adjacent to permanent water. This subcategory may eventually require subdivision).
2. *Stones* (includes stones and pebbles from about 1 cm to 1 m in diameter lying on open ground (level or sloping). This category also includes termitaria, dung-pats and similarly elevated objects, both natural and man-made).
    a. *Riparian* (a subdivision to specifically accommodate stones found along or in streams or rivers).
    b. *General* (ie. all 'stones' other than those associated with streams and rivers).
3. *Rocks* (includes large rocks and boulders, or sheets of rock forming part of an outcrop. Usually associated with vegetated hillsides or summits).
4. *Grass* (usually long (*ca.* >50 cm), reasonably uninterrupted expanses, but also includes grass associated with bushes and/or trees (ie. woodland or areas adjacent to forest patches) and does not exclude the presence of other types of smaller plants).
    a. *Within* (a subdivision to accommodate asilid species that perch within the grass layer rather than on its 'surface').
    b. *Tips* (a subdivision accommodating species that perch at the tips of grass stalks and hunt in the space above the grass layer rather than within it).

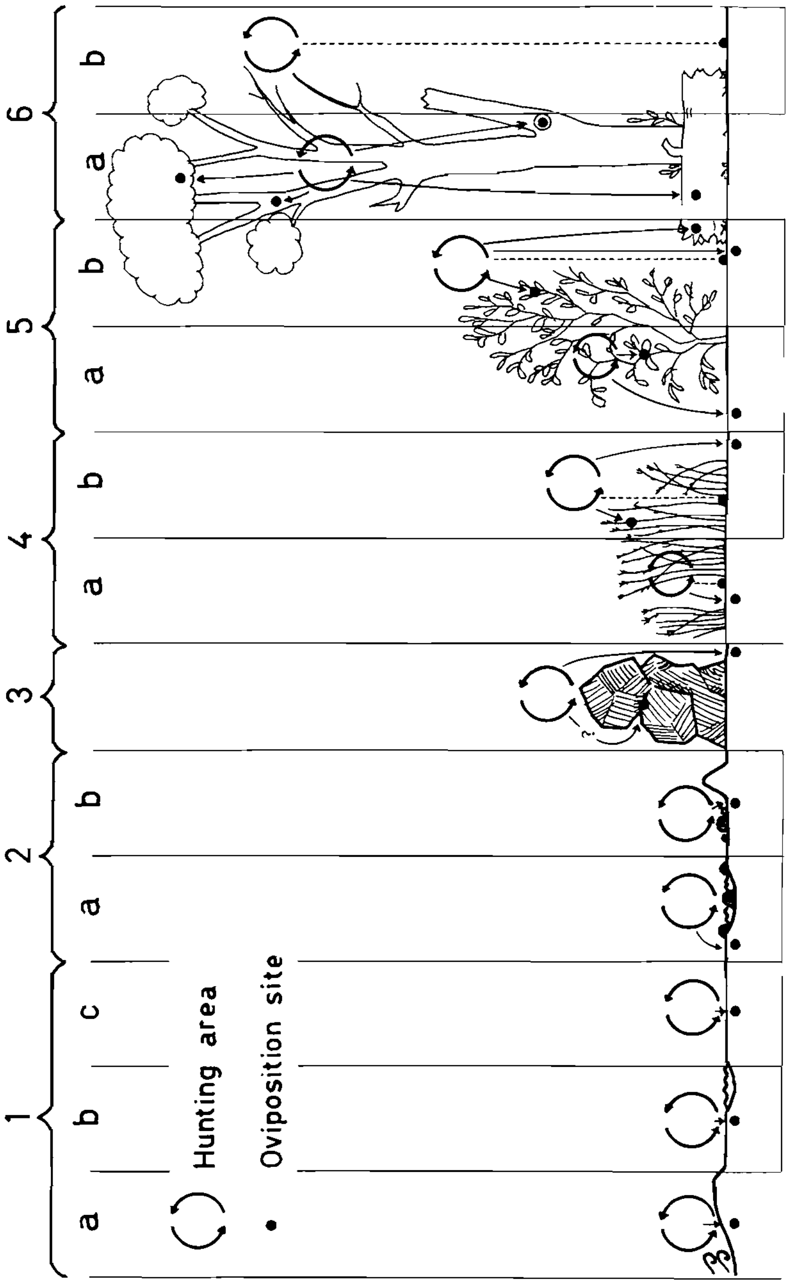

Fig. 2. Ecological categories of Afrotropical Asilidae. Numbers refer to primary divisions and letters to subdivisions of major categories as follows: 1. Ground (a. Beaches; b. River banks; c. General). 2. Stones (a. Riparian; b. General). 3. Rocks. 4. Grass (a. Within; b. Tips). 5. Shrubs & bushes (a. Within; b. Tips). 6. Trees (a. Within; b. Tips). Bold, circling arrows indicate hunting area utilised, solid dots indicate possible oviposition sites (fine arrows indicate females move to oviposition site, broken lines indicate eggs are dropped to the ground).

5. *Shrubs & bushes* (typically woody, usually broad-leafed, plants not exceeding *ca.* 2 m in height, and usually lacking an exposed trunk (as in trees). May be part of a forest understorey or margin, or of a more 'exposed' plant community).
    a. *Within* (a subdivision to accommodate asilid species that perch within the shrub or bush rather than on its 'surface').
    b. *Tips* (a subdivision accommodating species that perch on twigs and leaves situated on the outer surface of the shrub or bush and which hunt in the space above or adjacent to the plant).
6. *Trees* (includes large woody plants with exposed trunks and/or extensive canopies. May be 'exposed' as in woodland situations or part of a more closed forest community).
    a. *Within* (a subdivision to accommodate asilid species resting on the trunks or within the canopy).
    b. *Tips* (a subdivision accommodating species perching on twigs or leaves situated on the outer surface of the canopy).

Once these categories had been established, it became apparent that apart from feeding, oviposition was also well-supported by this classification. Although oviposition has not been observed in the vast majority of genera, oviposition strategies can be confidently inferred from ovipositor morphology as suggested by Melin (1923) in his pioneering work on Swedish asilids. A generic survey of ovipositor structure suggests that there are three main oviposition strategies within the family: i. Random egg-dropping; ii. Oviposition in sand or soil; iii. Oviposition on or in vegetation. Brief elaboration will provide the morphological criteria upon which these oviposition strategies are based.

Random egg-dropping: The female abdomen is circular in cross-section and the genital structures show no special adaptations for oviposition. The abdomen is usually rounded posteriorly, the terminal segments are not usually elongate, the cerci and subgenital plate are simple, and setae exhibit no unusual adaptations.

Oviposition in sand or soil: The female abdomen is circular in cross-section or dorsoventrally compressed (only occasionally somewhat laterally compressed). The postabdomen is adapted, in one or more ways, for depositing eggs into soil or under loose sand. These adaptations may take the form of elongated terminal segments, pointed and/or upturned cerci and/or subgenital plate, and/or the presence of stout spines or setae.

Oviposition on or in vegetation: The female abdomen is either circular in cross-section or distinctly laterally compressed (only occasionally somewhat dorsoventrally compressed). The postabdomen is adapted, in a variety of ways, for depositing eggs in crevices, grooves or holes in plant tissue. These adaptations may take the form of elongated terminal segments; when the cross-section is circular the diameter frequently diminishes progressively distally (the abdomen often being telescopic in structure). The cerci may take the form of an elongate extension of the postabdomen or be laterally compressed such that they form part of a knife-like ovipositor. When the ovipositor is not obviously elongate and/or laterally compressed the cerci may be elongate or equipped with long setae which serve to guide eggs into suitable situations.

An indication of the oviposition strategies usually practised within each ecological category proposed has been given in Fig. 2. Species which normally hunt from the ground surface always oviposit in sand or soil. Species inhabiting grass or bushes either drop their eggs at random to the ground, fly to the ground surface and deposit eggs there, or oviposit on the plants themselves. Tree frequenting species either drop their eggs to the ground or oviposit on or in the tree; as yet no examples of ground visiting species are known.

A further clue to oviposition behaviour may be provided by egg shape. Spherical eggs typify random egg-droppers while elongate-ovoid eggs are characteristic of species ovipositing in vegetation. Eggs of species which oviposit in soil are intermediate between these two extremes. Unfortunately egg shape is unknown for many genera of Afrotropical asilids. Although not yet attempted, it may be possible to infer oviposition behaviour from eggs dissected from gravid museum specimens.

ECOLOGICAL CLASSIFICATION OF AFROTROPICAL ASILIDAE

Using the ecological categories proposed above, the genera of Afrotropical Asilidae have been classified (Table 1). The outcome of this classification will now be discussed in greater detail. In this discussion lists of the genera assigned to each category have been included. The genera are arranged in the order they appear in Table 1, and within the same size groups indicated in Table 1 (ie. Small (S) – 5 or fewer described species; Medium (M) – 6–20 species; Large (L) – 21–50 species; Extra Large (X) – 51 or more species). These lists are useful in predicting which genera are most likely to be encountered in any particular ecological category.

Category 1. Ground

a. Beaches (marine – including adjacent sand dunes)

Included genera: *Neolophonotus* (X); *Philodicus* (L); *Hypenetes* (L); *Stichopogon* (M); *Prytania* (S); *Clinopogon* (S); *Rhadinus* (S).

Clinopogon appears to be the only truly beach-adapted asilid genus. It seems to be limited to the east coast of Africa as far south as Natal. Species are, like a variety of other beach inhabiting flies, cryptically coloured. Present evidence suggests that *Prytania* may also be limited to coastal sand dune situations in Namibia. Although *Stichopogon* is usually associated with sandy river banks, at least one southern African species has been collected on a Natal beach. *Philodicus* is a genus usually associated with damp conditions (wetlands, swamps, river banks). At least one species has, however, been collected on coastal sand-dunes. A few species of *Neolophonotus* and *Hypenetes* are found on dunes adjacent to the sea. At least some of these are, however, also found at sandy places further inland. *Rhadinus* is associated with dry, sandy, desert situations near water. The literature suggests that where desert sands meet the ocean, species may be found on beaches (Efflatoun 1937). It is noteworthy that it is members of the Stichopogoninae that are usually associated with beaches.

b. River banks (usually sandy)

Included genera: *Alcimus* (M); *Stichopogon* (M).

TABLE 1

Ecological classification of Afrotropical asilid genera. All genera are listed, even if no data exists for some, in order indicate areas requiring attention. Symbols and abbreviations: • = evidence from personal observation; ? = uncertain but probable; + = Egyptian data of Efflatoun (1934 1937); S = small (5 or fewer species); M = medium (6–20 species); L = large (21–50 species); X = extra large (51 and more species).

Taxonomic notes: *Promachus* (= *Bactria* - unpublished synonym); *Laphria* = *Choerades* (not yet verified for all Afrotropical species); for recently described genera of Stenogogoninae see Londt 1993*b* 1994*b*.

Ecological categories: 1a = Ground (*Beaches*); 1b = Ground (*River banks*); 1c = Ground (*General*); 2a = Stones (*Riparian*); 2b = Stones (*General*); 3 = Rocks; 4a = Grass (*Within*); 4b = Grass (*Tips*); 5a = Shrubs & bushes (*Within*); 5b = Shrubs & bushes (*Tips*); 6a = Trees (*Within*); 6b = Trees (*Tips*).

	Ecological categories												Genus
Apoleinae Lehr	1a	1b	1c	2a	2b	3	4a	4b	5a	5b	6a	6b	Size
Alcimus Loew	–	•	•	–	–	–	–	–	–	•	–	–	M
Apoclea Macquart	–	–	+	–	–	–	–	–	–	–	–	–	S
Dasophrys Loew	–	–	–	–	–	–	–	–	•	–	•	–	L
Dysclytus Loew	–	–	–	–	–	–	–	–	?	•	–	–	S
Gibbasilus Londt	–	–	–	–	–	–	–	–	–	•	–	–	S
Hippomachus Engel	–	–	–	–	–	–	–	–	–	–	•	–	M
Lycoprosopa Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
Neolophonotus Engel	•	–	•	•	•	•	–	•	–	•	•	–	X
Philodicus Loew	•	–	•	–	–	–	–	–	–	•	–	–	L
Promachus Meigen	–	–	–	–	•	–	•	–	–	•	–	–	X
Robertomyia Londt	–	–	–	–	–	–	–	–	–	–	–	–	S
Synolcus Loew	–	–	•	–	–	–	–	–	•	–	•	–	M
	2	1	5	1	2	1	1	1	2	6	4	0	
Asilinae Leach													
Astochia Becker	–	–	–	–	–	–	–	•	–	–	–	–	S
Cerdistus Loew	–	–	+	–	–	–	–	–	–	–	–	–	S
Cobalomyia Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
Congomochtherus Oldroyd	–	–	–	•	–	–	–	–	–	–	–	–	M
Dinozabrus Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
Erax Scopoli	–	–	–	–	–	–	–	–	–	–	–	–	S
Heligmonevra Bigot	–	–	–	–	–	–	–	–	•	–	–	–	L
Hoplopheromerus Becker	–	–	•	–	–	–	–	–	•	•	•	–	S
Machimus Loew	–	–	+	–	–	–	–	–	–	•	–	–	M
Neomochtherus Ost. Sack.	–	–	–	–	–	–	•	–	–	–	–	–	L
Rhadiurgus Loew	–	–	–	–	–	–	–	–	–	–	–	–	S
Senoprosopis Macquart	–	–	–	–	–	–	–	–	–	–	–	–	S
	0	0	3	1	0	0	1	1	2	2	1	0	
Dasypogoninae Macquart													
Caroncoma Londt	–	–	–	–	–	–	–	–	–	–	–	–	S
Pegesimallus Loew	–	–	•	–	–	–	•	–	•	–	–	–	L
Saropogon Loew	–	–	–	–	–	–	–	–	–	–	–	–	S
	0	0	1	0	0	0	1	0	1	0	0	0	
Laphriinae Macquart													
Atomosiini													
Dichaetothyrea De Meij.	–	–	–	–	–	–	–	–	–	–	–	–	S
Goneccalypsis Hermann	–	–	–	–	–	–	–	•	–	–	–	–	S
Loewinella Hermann	–	–	–	–	–	–	–	•	–	–	–	–	M
	0	0	0	0	0	0	0	2	0	0	0	0	

TABLE 1 (continued)

	Ecological categories												
Laphriini	1a	1b	1c	2a	2b	3	4a	4b	5a	5b	6a	6b	Genus size
Afromelittodes Old.& VB.	–	–	–	–	–	–	–	–	–	–	•	–	S
Andrenosoma Rondani	–	–	–	–	–	–	–	–	–	–	–	–	S
Anypodetus Hermann	–	–	•	–	–	–	–	–	–	–	–	–	M
Choerades Walker	–	–	–	–	–	–	–	–	–	•	–	•	L
Ctenota Loew	–	–	+	–	+	–	–	–	–	–	–	–	S
Dasyllina Bromley	–	–	–	–	–	–	–	–	–	–	–	–	S
Gerrolasius Hermann	–	–	–	–	–	–	–	•	–	–	–	–	S
Hyperechia Schiner	–	–	–	–	–	–	–	–	–	–	•	–	M
Katharma Oldroyd	–	–	–	–	–	–	–	–	–	–	–	–	S
Lamyra Loew	–	–	–	–	–	–	–	–	–	•	–	•	S
Laphyctis Loew	–	–	–	–	–	–	–	–	–	–	–	–	S
Laphystotes Oldroyd	–	–	•	–	–	–	–	–	–	–	–	–	S
Laxenecera Macquart	–	–	–	–	–	–	–	•	–	–	–	–	L
Nannolaphria Londt	–	–	–	–	–	–	–	–	–	•	–	–	S
Notiolaphria Londt	–	–	–	–	–	–	–	–	–	–	•	–	S
Nusa Walker	–	–	•	–	•	–	–	–	–	–	–	–	S
Orthogonis Hermann	–	–	–	–	–	–	–	–	–	–	–	–	S
Pilophoneus Londt	–	–	–	–	–	–	–	–	–	–	–	–	S
Proagonistes Loew	–	–	–	–	–	–	–	–	–	–	•	–	L
Prytania Oldroyd	•	–	•	–	–	–	–	–	–	–	–	–	S
Smeryngolaphria Hermann	–	–	–	–	–	–	–	–	–	–	–	–	S
Stiphrolamyra Engel	–	–	–	–	–	–	–	–	–	•	–	–	M
Storthyngomerus Hermann	–	–	–	–	–	–	–	–	–	•	–	–	S
Systropalpus Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
	1	0	5	0	2	0	0	2	0	5	4	2	
Laphystiinae Hardy													
Hoplistomerus Macquart	–	–	•	–	•	–	–	–	–	–	–	–	M
Perasis Hermann	–	–	–	–	–	–	–	–	–	–	–	–	S
Trichardis Hermann	–	–	•	–	•	–	–	–	–	–	–	–	M
	0	0	2	0	2	0	0	0	0	0	0	0	
Leptogastrinae Schiner													
Ammophilomima Enderlein	–	–	–	–	–	–	–	–	–	–	–	–	M
Dolichoscius Janssens	–	–	–	–	–	–	–	–	–	–	–	–	S
Euscelidia Westwood	–	–	–	–	–	–	–	•	–	•	–	•	L
Lasiocnemus Loew	–	–	–	–	–	–	–	•	–	–	–	–	M
Leptogaster Meigen	–	–	–	–	–	–	•	–	–	–	–	–	X
Lobus Martin	–	–	–	–	–	–	?	–	–	–	–	–	M
	0	0	0	0	0	0	1	2	0	1	0	1	
Ommatiinae Hardy													
Cophinopoda Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
Michotamia Macquart	–	–	–	–	–	–	–	–	–	–	–	–	S
Ommatius Wiedemann	–	–	–	–	–	–	•	–	–	•	–	•	X
Thallosia Oldroyd	–	–	–	–	–	–	–	–	–	–	–	–	S
	0	0	0	0	0	0	1	0	0	1	0	1	

TABLE 1 (continued)

	Ecological categories												Genus size
Stenopogoninae Hull	1a	1b	1c	2a	2b	3	4a	4b	5a	5b	6a	6b	
Acnephalum Macquart	–	–	●	–	●	–	–	–	–	–	–	–	M
Afroholopogon Loew	–	–	–	–	–	●	–	●	–	●	–	–	M
Agrostomyia Londt	–	–	●	–	–	–	●	–	–	–	–	–	S
Ammodaimon Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Anasillomos Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Ancylorhynchus Berthold	–	–	–	–	–	●	–	●	–	–	–	–	L
Bana Londt	–	–	–	–	–	–	–	●	–	●	–	–	S
Connomyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	M
Corymyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Danomyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	M
Daspletis Loew	–	–	●	–	–	–	–	–	–	–	–	–	M
Dioctobroma Hull	–	–	–	–	–	–	–	–	–	–	–	–	S
Dogonia Oldroyd	–	–	–	–	–	–	–	–	–	–	–	–	S
Empodiodes Oldroyd	–	–	●	–	–	–	–	–	–	–	–	–	S
Gonioscelis Schiner	–	–	●	–	–	●	–	●	–	●	–	–	L
Habropogon Loew	–	–	●	–	–	–	–	–	–	–	–	–	S
Hermannomyia Oldroyd	–	–	●	–	–	–	–	–	–	–	–	–	S
Hynirhynchus Lindner	–	–	?	–	–	–	–	–	–	–	–	–	S
Hypenetes Loew	●	–	●	–	–	●	–	●	–	–	–	–	L
Irwinomyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Lycostommyia Oldroyd	–	–	–	–	–	●	–	–	–	–	–	–	M
Macroetra Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Microphontes Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Microstylum Macquart	–	–	–	–	–	●	–	●	–	●	–	–	X
Oratostylum Ricardo	–	–	–	–	–	–	–	–	–	–	–	–	S
Pedomyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	M
Pycnomerinx Hull	–	–	–	–	–	–	–	●	–	–	–	–	S
Remotomyia Londt	–	–	●	–	–	–	–	–	–	–	–	–	S
Rhabdogaster Loew	–	–	–	–	–	–	–	●	–	–	–	–	M
Rhacholaemus Hermann	–	–	●	–	–	–	–	–	–	–	–	–	S
Scylaticus Loew	–	–	●	–	–	–	–	●	–	●	–	–	L
Sisyrnodytes Loew	–	–	●	–	●	●	–	–	–	–	–	–	M
Stenopogon Loew	–	–	–	–	–	–	–	–	–	●	–	–	M
Teratopomyia Oldroyd	–	–	–	–	–	–	–	–	–	?	–	–	S
Trichoura Londt	–	–	●	–	–	–	–	–	–	–	–	–	M
	1	0	22	0	2	7	1	9	0	6	0	0	
Stichopogoninae Hardy													
Clinopogon Bezzi	●	–	–	–	–	–	–	–	–	–	–	–	S
Rhadinus Loew	+	–	+	–	–	–	–	–	–	–	–	–	S
Sporadothrix Hermann	–	–	–	–	–	–	–	–	–	–	–	–	S
Stichopogon Loew	●	●	–	●	–	–	–	–	–	–	–	–	M
	3	1	1	1	0	0	0	0	0	0	0	0	
Trigonomiminae Enderlein													
Damalis Fabricius	–	–	–	–	–	–	●	●	–	●	–	●	L
Oligopogon Loew	–	–	–	–	–	–	–	●	–	–	–	–	M
Oxynoton Janssens	–	–	–	–	–	–	–	–	–	–	–	–	S
Rhipidocephala Hermann	–	–	–	–	–	–	–	●	–	–	–	–	L
	0	0	0	0	0	0	1	3	0	1	0	1	
Grand totals:	[7	2	39]	[3	8]	[8]	[7	20]	[5	22]	[9	5]	
		48		**11**		**8**	**27**		**27**		**14**		

The survival of *Stichopogon* is clearly dependant on damp sand and adults are most commonly found on sandy river banks. They have also been found on paths through damp, sandy, coastal dune-forests. The suggested association of *Alcimus* with river banks is largely based on specimens collected along the banks of the Orange River (Upington area), or associated with dunes near rivers in the northern Cape Province. As these species feed primarily on grasshoppers, which may be concentrated in better vegetated areas along water courses in otherwise arid areas, the association may be indirect.

The diversity of ground-inhabiting asilids restricted to the banks of streams, rivers and lakes is extremely low. The reasons for this probably include factors relating to the unreliable nature of streams in more arid areas, the almost total absence of lakes in Africa, inadequate adaptation of eggs and larvae to dry conditions (as experienced during drought) or flooding, and the competition offered by Odonata and other riverine predators.

c. General

Included genera: *Neolophonotus* (X); *Philodicus* (L); *Pegesimallus* (L); *Gonioscelis* (L); *Hypenetes* (L); *Scylaticus* (L); *Alcimus* (M); *Synolcus* (M); *Machimus* (M); *Anypodetus* (M); *Hoplistomerus* (M); *Trichardis* (M); *Acnephalum* (M); *Connomyia* (M); *Danomyia* (M); *Daspletis* (M); *Pedomyia* (M); *Sisyrnodytes* (M); *Trichoura* (M); *Apoclea* (S); *Cerdistus* (S); *Hoplopheromerus* (S); *Ctenota* (S); *Laphystotes* (S); *Nusa* (S); *Prytania* (S); *Agrostomyia* (S); *Ammodaimon* (S); *Anasillomos* (S); *Corymyia* (S); *Empodiodes* (S); *Habropogon* (S); *Hermannomyia* (S); ?*Hynirhynchus* (S); *Irwinomyia* (S); *Macroetra* (S); *Microphontes* (S); *Remotomyia* (S); *Rhacholaemus* (S); *Rhadinus* (S).

It is clear that many asilid genera are adapted for life on open ground. The species which restrict themselves to this situation are frequently small and cryptic. Most of the genera listed above fit this description. There are, however, a number of asilids which make use of open ground for only part of their lives. They may visit the open ground in order to oviposit (eg. some *Pegesimallus*, *Agrostomyia*) or to benefit from the relatively higher temperatures experienced by unshaded, open areas of ground (eg. some *Neolophonotus*, *Synolcus*, *Gonioscelis*, *Machimus*, *Hoplopheromerus*). Virtually any asilid may find itself on the ground when tackling a heavy prey item or when disturbed. Such cases are clearly 'accidental'.

The diversity of asilids is highest in this category and probably reflects the arid-adapted nature of the family as a whole and the fact that most species have subterranean larvae.

Category 2. Stones

a. Riparian

Included genera: *Neolophonotus* (X); *Congomochtherus* (M); *Stichopogon* (M).

It is interesting to note that a number of asilid species appear to be adapted for hunting from the exposed tops of stones in streams or along the banks of streams.

Congomochtherus, in particular, appears to be highly adapted to this biotope, while a few species of *Neolophonotus* (eg. *N. io* Londt) and *Stichopogon* (eg. *S. unicolor* Ricardo) are also found in this restricted situation. While not known for certain, it is assumed that the females of these species use damp sand along the stream margins for oviposition.

Although this highly specialised habitat category has been identified, it may suggest that a number of the other more broadly defined categories may eventually be refined, leading to the recognition of other more restricted subdivisions.

b. General (includes termitaria, dung and other elevated objects)

Included genera: *Neolophonotus* (X); *Promachus* (X); *Hoplistomerus* (M); *Trichardis* (M); *Acnephalum* (M); *Sisyrnodytes* (M); *Ctenota* (S); *Nusa* (S).

This habitat category is probably a natural extension of open ground (1c). Certainly, a number of ground-inhabiting species are also known to perch on stones. The only genus listed which is not included in habitat 1c is *Promachus*. While a number of species of *Promachus* (eg. the *amastrus* species group) are commonly found resting on large stones and termitaria, I cannot recall ever seeing them on open ground. Although more observations are required, it appears that some species of *Acnephalum* and *Sisyrnodytes* may prefer to perch on small stones rather than on open ground. The females of species in this category almost certainly visit the ground to oviposit, although some species do not appear to have any special adaptations for digging, so may merely drop their eggs to the ground. Species of *Hoplistomerus* are exceptional in that they are usually found perching on bovine dung, waiting for approaching dung beetles, which constitute their principal prey (Bernon 1981). They are, however, also found on stones. Dung may eventually require its own subcategory, as it may prove to be a unique habitat for asilid larval development.

Category 3. Rocks

This category includes rocks, large boulders, rocky slopes, cliffs and rocky summits of hills.

Included genera: *Neolophonotus* (X); *Microstylum* (X); *Ancylorhynchus* (L); *Gonioscelis* (L); *Hypenetes* (L); *Afroholopogon* (M); *Lycostommyia* (M); *Sisyrnodytes* (M).

As with open ground, it is possible that some species found resting on rocks are there temporarily. They may be visiting in order to benefit from the ability rocks have of retaining heat when the air temperature drops. Possible examples may be species of *Ancylorhynchus*, *Gonioscelis* and *Lycostommyia*. Clear associations with rocks exist for *Hypenetes* and some *Afroholopogon* (a recently erected genus to accommodate Afrotropical species previously placed in *Heteropogon* and *Holopogon* – see Londt 1994*a*). There are also a number of small *Neolophonotus* species which are consistently found frequenting rocks. As in the case of asilids living on riparian rocks, it is assumed that females visit the ground for oviposition, although the use of cracks in boulders cannot be excluded. The occurrence of some large, wide-ranging *Microstylum* species on rocks is probably without significance.

Category 4. Grass

a. Within

Included genera: *Promachus* (X); *Leptogaster* (X); *Ommatius* (X); *Neomochtherus* (L); *Pegesimallus* (L); *Damalis* (L); ?*Lobus* (M); *Agrostomyia* (S).

Some fairly large, wide-ranging asilids commonly use thick grass stems as perches (eg. some *Promachus*). However, while they may occasionally venture beyond the confines of long grass, there are a number of species which appear to be largely restricted to this biotope. Many species of *Leptogaster*, and probably the closely related *Lobus*, as well as species of *Neomochtherus* are known to hunt within the confines of long grass. Some species of *Damalis* (eg. *D. femoralis* Ricardo) perch on grass stems, much like *Leptogaster*, and probably feed both within the grass layer and above it. A few of the smaller species of *Pegesimallus* (eg. *niger* Bromley) are commonly found in grass (usually on stems which are bent over, offering a horizontal perch). While members of this genus may forage in the spaces between grass tussocks, they may also feed on prey within the grass layer itself. Like many of the species hunting from the tips of grass stems, most of those in this category merely drop their eggs to the ground (eg. *Leptogaster* and *Damalis*). *Pegesimallus* species visit the ground for oviposition, as probably do some *Promachus*. *Neomochtherus* species, however, probably lodge eggs in natural crevices in the grass as they possess suitably adapted ovipositors.

b. Tips

Included genera: *Neolophonotus* (X); *Microstylum* (X); *Laxenecera* (L); *Euscelidia* (L); *Ancylorhynchus* (L); *Gonioscelis* (L); *Hypenetes* (L); *Scylaticus* (L); *Damalis* (L); *Rhipidocephala* (L); *Loewinella* (M); *Lasiocnemus* (M); *Afroholopogon* (M); *Rhabdogaster* (M); *Oligopogon* (M); *Astochia* (S); *Goneccalypsis* (S); *Gerrolasius* (S); *Bana* (S); *Pycnomerinx* (S).

While there is some overlap with category 4a since some species perch both at the tips of grass stems and lower down, some members of the genera listed above usually rest on the tips of grass stalks and forage in the air space immediately above the grass layer. Larger species of *Neolophonotus*, *Microstylum*, *Gonioscelis*, *Hypenetes*, *Scylaticus* and *Bana* tend to be far-ranging and merely use grass tips as convenient resting places. As these species may also use shrubs within grassland situations, they are probably not specifically adapted for hunting from the tops of grass stems. Species of some genera visit the ground to oviposit, such as *Afroholopogon*, *Rhabdogaster*; *Oligopogon* and *Pycnomerinx*, as testified by their acanthophorites and scoop-like subgenital-plates. Like *Leptogaster*, grass-tip frequenting *Euscelidia*, *Damalis*, *Rhipidocephala*, *Loewinella*, *Lasiocnemus* and *Goneccalypsis* have simple unspecialised ovipositors and probably drop their eggs at random from their perches, thus avoiding visits to the ground. Species of *Astochia*, although seen resting at the tips of tall grass stems in Malaŵi (eg. *A. armata* (Becker)), is exceptional in that it possesses an elongate, telescopic ovipositor and probably deposits its eggs in vegetation.

Category 5. Shrubs & bushes

This category includes thick undergrowth formed by a mosaic of bushes, shrubs and long grass, as well as the woody vegetation characteristic of the winter-rainfall areas of the south-western Cape Province (known as macchia or fynbos).

a. Within

Included genera: *Dasophrys* (L); *Heligmonevra* (L); *Pegesimallus* (L); *Synolcus* (M); ?*Dysclytus* (S); *Hoplopheromerus* (S).

Although this category may overlap 5b, 6a and 6b, it is here kept separate. The apocleine and asiline genera listed (*Dasophrys*, *Heligmonevra*, *Synolcus* and *Dysclytus*) possess laterally compressed ovipositors. These are well adapted for oviposition in vegetation and so may be more adapted to life in bushes than the other genera listed. *Pegesimallus*, although commonly found in thick undergrowth, has acanthophorites and is known to visit the ground to oviposit. Little is known of the biology of *Hoplopheromerus*, which has been encountered in the under-storey of west African rain-forests (eg. *H. podagricus* Bezzi). As they have also been seen resting on the ground, they may deposit their eggs there, as the ovipositor is not obviously adapted for oviposition in vegetation.

b. Tips

Included genera: *Neolophonotus* (X); *Promachus* (X); *Ommatius* (X); *Microstylum* (X); *Philodicus* (L); *Choerades* (L); *Euscelidia* (L); *Gonioscelis* (L); *Scylaticus* (L); *Damalis* (L); *Alcimus* (M); *Machimus* (M); *Stiphrolamyra* (M); *Afroholopogon* (M); *Stenopogon* (M); *Dysclytus* (S); *Gibbasilus* (S); *Hoplopheromerus* (S); *Lamyra* (S); *Nannolaphria* (S); *Storthyngomerus* (S); *Bana* (S); ?*Teratopomyia* (S).

The genera listed above may be further grouped in accordance with their more specific habits. The majority of species belonging to *Promachus*, *Neolophonotus*, *Microstylum*, *Philodicus*, *Gonioscelis*, *Scylaticus*, *Alcimus*, *Machimus*, *Stiphrolamyra*, *Afroholopogon*, *Stenopogon*, *Lamyra* and *Bana* merely rest on the upper parts of bushes. These species are usually wide-ranging and probably use bushes only as convenient resting places. A number of species are found resting on broad leaves, usually on the sides of bushes and trees on forest margins or along forest paths (ie. *Choerades*, *Hoplopheromerus*, *Nannolaphria*, *Storthyngomerus*). Then there are those species which perch at the tips of twigs (ie. not on leaves) on the outer 'surface' of bushes (ie. *Ommatius*, *Euscelidia*, *Damalis*, *Gibbasilus* and *Teratopomyia*). These species tend to hawk repeatedly from the same perch (ie. they dart at prey and return with or without it to the same perch). For the present, these groups are combined until the significance of their different behaviours is better understood.

Category 6. Trees

a. Within (on trunks, branches and twigs)

Included genera: *Neolophonotus* (X); *Dasophrys* (L); *Hippomachus* (M); *Proagonistes* (L); *Synolcus* (M); *Hyperechia* (M); *Hoplopheromerus* (S); *Afromelittodes* (S); *Notiolaphria* (S).

Although members of the listed genera frequent spaces within trees, they are usually large asilids which fly freely from one tree to another (a possible exception being *Notiolaphria*). Subgroups may be recognised based on oviposition strategy and subsequent development of immatures. These include a group which oviposit on the trees themselves (in bark crevices or between leaves), and include some *Neolophonotus* (highly specialised species like *N. dichaetus* Hull cement their eggs between the leaves of certain leguminous trees), *Dasophrys*, *Hippomachus* and *Synolcus* (all members of Apocleinae). Larvae hatching from eggs of these species probably fall to the ground and undergo further development subterraneously. Another group, which includes *Hyperechia* with its unusual 'cleptoparasitic' development in carpenter bee nests, oviposit on or in dead wood. The larvae develop within the wood (often in the galleries of wood-boring insects). Although little or nothing is known of the oviposition behaviour of *Proagonistes* and *Afromelittodes*, they may be similar to *Hyperechia* (all three belong to the same tribe – the Laphriini). Little is known of *Notiolaphria* and *Hoplopheromerus*. *Notiolaphria* has been collected from the trunks of dead trees (horizontal logs on the ground in forest situations), while *Hoplopheromerus* adults have been found resting on the twigs and thin branches of spindly trees in west African (Ivory Coast) rain-forest. There is no evidence of any species in this group merely dropping their eggs to the ground or visiting the ground for oviposition.

b. Tips

Included genera: *Ommatius* (X); *Choerades* (L); *Euscelidia* (L); *Damalis* (L); *Lamyra* (S).

This category may merely be an extension of 5b, the difference being only the height above the ground. All the genera listed, except *Choerades*, possess unspecialised ovipositors suggesting that they may merely drop their eggs to the ground. *Choerades*, on the other hand, is a genus that almost certainly has its larval development in wood, like the other Laphriini mentioned under 6a. Unlike *Ommatius*, *Euscelidia* and *Damalis*, *Choerades* does not perch at the tips of dead twigs, but rests on the upper surfaces of leaves (often in sunny situations). Adult *Lamyra* have been observed perching on the 'outside surface' of trees, including Acacias. These large, wasp-like asilids appear to range over large areas and are probably not restricted to hunting from trees (and bushes), but merely use these as convenient perches.

BEHAVIOURAL TRENDS WITHIN ASILID SUBFAMILIES

As there appear to be certain consistencies in behaviour within the traditionally defined asilid subfamilies (Table 1, Fig. 3), it is useful to comment briefly on these trends at the risk of some repetition.

Apocleinae: Members of this subfamily display a clear tendency to hunt from exposed positions on the outer surfaces of bushes and shrubs, from tree trunks and branches, or from the surface of open ground. There also appear to be two groups within the subfamily in terms of oviposition strategy – those which deposit eggs directly into soil, and those which deposit eggs in vegetation above ground. As extralimital evidence suggests that larvae of Apocleinae commonly feed on subterranean beetle larvae, asilid larvae hatching from eggs laid in bushes and trees must fall to the ground. This is presumably an adaptation for dispersal. Ground-inhabiting species demonstrate clear adaptations for oviposition in soil. *Alcimus*, *Philodicus* and to a lesser extent *Promachus*, have strong tubular ovipositors, usually equipped with stout spines. Many ground residing species of *Neolophonotus* have strong, upwardly directed, spine-like cerci to aid in soil oviposition, while plant-inhabiting species have laterally compressed ovipositors adapted to oviposition in vegetation (ie. the *suillus* species group).

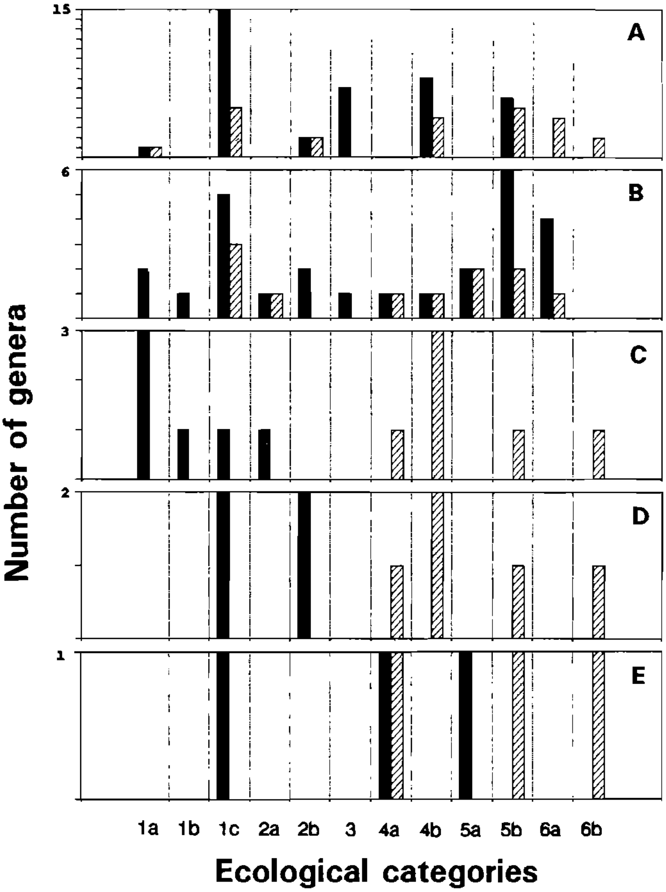

Fig. 3. Visual comparison of ecological categories occupied by genera in Afrotropical asilid subfamilies.
A – Stenopogoninae (solid), Laphriinae (hatched)
B – Apocleinae (solid), Asilinae (hatched)
C – Stichopogoninae (solid), Trigonomiminae (hatched)
D – Laphystiinae (solid), Leptogastrinae (hatched)
E – Dasypogoninae (solid), Ommatiinae (hatched)

Asilinae: The trend here appears to be similar to the Apocleinae, except that adaptation to an arboreal life-style is less marked. This subfamily is relatively poorly represented in southern Africa.

Dasypogoninae: Although little data is available, observations on the large and commonly encountered *Pegesimallus* indicate that species in this group hunt from grass or other dense vegetation (in some instances from the ground surface eg. *P. laticornis* Loew), and that females oviposit just below the surface of sand and soil.

Laphriinae: The two recognised tribes (combined in Fig. 3) appear to differ as follows.

Atomosiini: While this tribe is poorly represented in the Afrotropical Region, the limited data available for the two African genera suggest that these small flies are most commonly encountered at the tips of medium to long grass stalks. As females demonstrate no obvious adaptations of the ovipositor, it is likely that they drop their eggs at random in vegetation, and that larval development takes place in the soil.

Laphriini: Data suggest that species in this tribe are found in a variety of situations, ranging from open ground to the tips of grass stalks and to the leaves, branches and trunks of bushes and trees. This range is matched by a range in ovipositor form. *Hyperechia* is known to oviposit on dead wood (including untreated structural timber) adjacent to the nests of carpenter bees (*Xylocopa*), and there are non-Afrotropical records suggesting that a number of other genera (eg. *Andrenosoma* & *Pogonosoma*) have similar oviposition behaviour, but that their maggots feed on the larvae of wood-boring insects, mostly beetles (Lavigne, Denis & Gowen 1978). The ovipositor of *Hyperechia* is conical with an elongate, rather tubular terminal part (formed by cerci and hyperproct), which is presumably an adaptation for oviposition in wood-crevices or holes. *Andrenosoma*, *Choerades*, *Dasyllina*, *Proagonistes* and *Storthyngomerus* share this ovipositor form and are also found in association with woody plants. It is reasonable to suggest that species of these genera probably have a life-style somewhat like that of *Hyperechia*, although their larvae probably feed mainly on coleopterous larvae. Other genera known to be associated with bushes and trees are *Afromelittodes*, *Lamyra*, *Stiphrolamyra*, *Nannolaphria* and *Notiolaphria*. The last two genera, like those already discussed, are found in forests. The ovipositor of *Notiolaphria* is equipped with long, stiff terminal setae, which together form a tube-like funnel through which an egg could pass. Species of this genus may also have wood-inhabiting larvae. *Nannolaphria* has a simple ovipositor which suggests that its life-style may be rather different from the genera already discussed. Those genera known to inhabit grassland situations (*Gerrolasius* and *Laxenecera*) have simple ovipositors and may merely drop their eggs to the ground. The balance of genera inhabit open ground, sometimes using stones as perches. The species in these genera, except *Ctenota*, have simple ovipositors. *Ctenota* has a somewhat laterally compressed ovipositor which may be an adaptation for digging. *Nusa* is the only other genus in which there may be adaptation for digging; species have a row of long, strong setae on the hind margin of the last well-developed tergite. The ground associated genera lacking obvious adaptations to the ovipositor (*Anypodetus*, *Laphystotes* and *Prytania*) presumably have simple oviposition strategies, which may merely involve placing eggs on the ground surface or at the interface between stones and ground.

Laphystiinae: Genera of this subfamily are clearly similar to the unspecialised ground and pebble inhabiting Laphriini just discussed. Although their ovipositors are simple and unspecialised, the fact that at least some species of *Hoplistomerus* (eg. *H. nobilis* Loew) are closely associated with bovine dung (feeding almost exclusively on dung-visiting Scarabaeidae), may suggest that at least a few species oviposit in dung, and that no ovipositor adaptation is necessary to expedite this behaviour.

Leptogastrinae: Data suggest that all genera of this subfamily perch on vertical grass stems or at the tips of twigs on the outer surfaces of bushes or trees. The whole thoracic structure is suggestive of adaptation to such perching. The arrangement of legs (where those in front are short and those at the back are long) precludes them from moving about on the ground surface. The elongated body form is also an adaption for hovering flight and species probably hunt on the wing rather than observing passing prey from a surveillance perch. Ovipositors are simple (and the eggs spherical), and so it is clear that species in this group merely drop their eggs to the ground.

Ommatiinae: Little is known of the behaviour of genera in this group. Species of *Ommatius* are found in very similar places to those of Leptogastrinae. As the ovipositor form is also of a simple, unspecialised kind, these species may also drop their eggs to the ground.

Stenopogoninae: Genera of this subfamily are clearly associated with the ground surface. Those which have been seen perching on rocks and vegetation are usually large, wide-ranging species which would be equally at home on the ground. As the possession of acanthophorites (setae-equipped cerci) is diagnostic of the subfamily, it is likely that all stenopogonines oviposit in sand or soil.

Stichopogoninae: The close association with damp, sandy situations is an obvious feature of the subfamily. The female hypandrium is laterally compressed and scoop-shaped, while the cerci are equipped with strong setae (acanthophorites), suggesting adaptation for oviposition in sand.

Trigonomiminae: Members of this subfamily share the same habitats and ovipositor design as the Leptogastrinae. As grass-stalk and twig-tip perchers they drop their eggs to the ground.

ECOLOGICAL CATEGORIES AND PREY PREFERENCES

Although some prey records have appeared in a number of publications (see review above), these are isolated and have never been used to inform us on possible trends within the traditional taxonomic classification, or within any identified habitats. Accumulated data from Natal Museum specimens, together with Hobby's (1935) published information for Zimbabwe, has now been processed and stored in a database. Although a total of only 1608 prey records are available, a preliminary survey of prey preferences, resolved at generic level, is possible (Table 2).

Apocleinae: Data suggest that included genera are reasonably unselective in their eating habits. Not only are they known to feed on a wide range of prey, but the larger insect orders are best represented.

Asilinae: Inadequate data preclude meaningful comment. The paucity of available information is probably due to the relatively poor representation of this subfamily in southern Africa (where the majority of prey records were obtained).

Dasypogoninae: The only genus for which information is available is *Pegesimallus*,

TABLE 2

Survey of prey preferences of Afrotropical Asilidae, based on 1608 records. Genera for which there is no information are excluded. Abbreviations: – = no records; • = 1–5 records; • = 6–20 records; • = 21–50 records; • = >50 records. [Hym = Hymenoptera, Dip = Diptera, Orth = Orthoptera, Cole = Coleoptera, Hem = Hemiptera, Lepi = Lepidoptera, Iso = Isoptera, Neuro = Neuroptera.]

	Prey									
	Hym	Dip	Orth	Cole	Hem	Lepi	Iso	Neuro	Aranina	Other
Apocleinae Lehr										
Alcimus Loew	•	•	•	•	•	•	•	•	–	•
Dasophrys Loew	•	•	•	•	•	–	•	–	–	–
Dysclytus Loew	–	–	–	•	–	–	–	–	–	–
Neolophonotus Engel	•	•	•	•	•	•	•	•	•	•
Philodicus Loew	•	•	•	•	•	•	–	•	–	•
Promachus Meigen	•	•	•	•	•	•	–	–	–	–
Synolcus Loew	–	–	•	–	–	–	–	–	–	–
Asilinae Leach										
Congomochtherus Oldroyd	–	•	–	–	–	–	–	–	–	–
Heligmonevra Bigot	–	–	–	–	•	•	–	–	–	–
Hoplopheromerus Becker	–	–	–	–	•	–	–	–	–	–
Neomochtherus Ost. Sack.	•	•	–	•	•	•	–	–	–	–
Dasypogoninae Macquart										
Pegesimallus Loew	•	•	–	•	•	•	•	–	•	•
Laphriinae Macquart										
Afromelittodes Old.& VB	•	–	–	–	–	–	–	–	–	–
Anypodetus Hermann	•	•	–	–	–	–	–	–	–	–
Choerades Walker	•	•	–	•	–	–	–	–	–	–
Hyperechia Schiner	•	–	–	–	–	–	–	–	–	–
Lamyra Loew	•	•	–	–	–	–	–	–	–	–
Laphyctis Loew	–	–	–	–	•	–	–	–	–	–
Laphystotes Oldroyd	•	•	–	–	–	–	–	–	–	–
Laxenecera Macquart	•	•	•	•	•	–	–	–	–	–
Nannolaphria Londt	•	•	–	–	•	–	–	–	–	–
Nusa Walker	•	–	•	–	–	•	–	–	–	–
Proagonistes Loew	•	–	–	–	–	•	–	–	–	–
Prytania Oldroyd	–	•	–	–	–	–	–	–	–	–
Stiphrolamyra Engel	•	•	–	•	•	–	–	–	–	–
Laphystiinae Hardy										
Hoplistomerus Macquart	–	•	–	•	–	–	–	–	–	–
Trichardis Hermann	•	–	–	–	–	–	–	–	–	–
Leptogastrinae Schiner										
Euscelidia Westwood	•	•	–	–	•	•	–	–	•	•
Lasiocnemus Loew	–	–	–	–	–	–	–	–	•	–
Ommatiinae Hardy										
Ommatius Wiedemann	–	•	–	•	•	–	–	–	–	–
Stenopogoninae Hull										
Acnephalum Macquart	•	–	–	•	•	–	–	–	–	–
Afroholopogon Londt	•	•	–	•	•	–	–	–	–	–
Ancylorhynchus Berthold	•	–	–	–	–	–	–	–	–	–
Bana Londt	•	–	–	–	–	–	–	–	–	–
Daspletis Loew	•	•	•	–	•	•	–	–	•	–
Gonioscelis Schiner	•	•	–	•	•	•	•	–	–	–
Hypenetes Loew	•	–	–	•	–	–	–	–	–	–
Microstylum Macquart	•	•	•	•	•	–	•	•	–	•
Oratostylum Ricardo	•	–	•	–	–	•	–	–	–	–
Rhabdogaster Loew	•	•	–	–	•	–	–	–	•	–
Rhacholaemus Hermann	–	•	–	–	–	–	–	–	–	–
Scylaticus Loew	•	•	–	–	•	–	–	–	–	•
Sisyrnodytes Loew	•	–	–	•	–	–	–	–	–	–
Stenopogon Loew	•	•	–	–	–	–	–	–	–	–
Teratopomyia Oldroyd	–	–	–	•	–	–	–	–	–	–
Stichopogoninae Hardy										
Clinopogon Bezzi	–	–	–	–	•	–	–	–	–	–
Stichopogon Loew	•	•	–	–	–	–	–	–	–	–
Trigonomiminae Enderlein										
Damalis Fabricius	•	•	–	•	•	–	–	–	•	•
Rhipidocephala Hermann	•	•	•	–	–	–	–	–	–	–

the species of which appear to have catholic tastes. There is, however, an inexplicable absence of Orthoptera in their diet.

Laphriinae: No data exist for genera of Atomosiini. While limited information is available for Laphriini, it appears that members of this group feed on a wide range of prey. There does appear to be a slight tendency to favour Hymenoptera. As many species in this tribe appear to mimic Hymenoptera, it is possible that some special correlation exists.

Laphystiinae: The majority of prey records for this group belong to a single species, *Hoplistomerus nobilis* Loew, which is clearly a specialist feeder on dung visiting Scarabaeidae. The Natal Museum prey database does not include all 150 records reported by Bernon (1981), although it does contain some of them (specimens donated to the museum). Bernon's (1981) data is the best available and shows the following prey breakdown – Coleoptera (145 records), Diptera (2 records), Hemiptera (2 records), Hymenoptera (1 record). Of the Coleoptera records only 10 were not Scarabaeidae; these being Hydrophilidae (6), Histeridae (1), Staphylinidae (2) and Curculionidae (1). This feeding speciality is entirely consistent with the species' habit of perching on the upper surfaces of dung-pats (usually bovine).

Leptogastrinae: Available records are limited to *Leptogaster* and *Lasiocnemus*. While the former may have a wide range of prey, the few records of the latter are all spiders. The prey hunting behaviour of *Lasiocnemus lugens* Loew was witnessed during a trip to Swaziland. Adult flies appear to search the seeding heads of tall grasses for spiders. Once a spider has been located, the fly darts at it, grabbing it from its web and retreating to a nearby grass stalk to feed. This behaviour is different from the usual habit of asilids, which is to perch and await flying insect prey, which are then attacked on the wing and brought back to the perch to be consumed. It is not known whether the unusual behaviour seen in *Lasiocnemus* is common to the whole subfamily.

Ommatiinae: Prey records are limited to *Ommatius*. Although these flies are fairly common, too few prey records exist to allow comment.

Stenopogoninae: Genera of this subfamily feed on a wide variety of prey. Although there is a slight tendency towards taking Hymenoptera, there are two notable exceptions. *Gonioscelis* actively feeds on Coleoptera (flower visiting Scarabaeidae), and the well-developed fore femora characteristic of the genus, may be an adaptation for this diet. The majority of prey records for *Scylaticus* are Hemiptera (Lygaeidae).

Stichopogoninae: Prey records for members of this subfamily are too few to allow comment.

Trigonomiminae: The majority of prey records for this subfamily belong to a single species, *Damalis femoralis* Ricardo, and have been discussed by Londt (1991). Apart from an absence of Orthoptera, the species appears to have catholic tastes.

Available evidence suggests, apart from a few exceptions, that Afrotropical asilids appear to be opportunistic feeders, capturing virtually anything of suitable size within their particular habitats. Unfortunately this kind of information is largely unhelpful when attempting any kind of ecological analysis. A serious limitation exists when dealing with prey preferences at generic level; the specific adaptations which almost certainly exist within each genus are largely masked. For example, *Alcimus* is shown as feeding primarily on Orthoptera and Lepidoptera. Although true at generic level, what is not appreciated is that some species, those associated with open ground (ecological categories 1b and 1c), account for most of the orthopteran records, while those species inhabiting the outer edges of bushes (ecological category 5b) account for the majority of lepidopterans. Although it is beyond the scope of this paper and current data, I believe that when all taxonomic problems have been resolved, and when many more prey records are established, the relationship between prey preference and ecological category may become a valuable means of defining the ecological roles played by Afrotropical Asilidae.

DISCUSSION

While being far from perfect, the suggested ecological classification of Afrotropical asilid genera is commendable. Although some overlap probably exists between the categories and sub-categories identified, they serve as an initial, albeit broad, means of grouping genera according to where species are normally found.

The only African situation not immediately identifiable with the proposed scheme is the 'fynbos' or 'macchia' vegetation characteristic of the winter-rainfall, Mediterranean climatic region of the south-western Cape Province. This is not problematic as this low, woody vegetation equates well with the bushes and trees found of other regions. Convincing support for this is found when tree-inhabiting apocleine genera such as *Dasophrys* and *Synolcus* are examined. Large species of both genera are found in places where woody plants are sizeable (eg. *D. natalensis* (Ricardo) and *S. dubius* (Macquart) found in the evergreen forests of Natal), while small species are invariably associated with the small woody plants of the Cape macchia (eg. *D. nigricans* (Wiedemann) and *S. acrobaptus* (Wiedemann)). Examples of intermediate sized species living in intermediate sized plants are numerous. Bush-inhabiting *Pegesimallus* (Dasypogoninae) demonstrate the same size phenomenon. Thus *P. pedunculatus* (Loew) is a large species associated with large bushes in summer rainfall areas, while *P. tapulus* (Walker) is an example of a small macchia-inhabiting species. A detailed examination of these and other genera occurring in both the Cape macchia and larger bushes and trees in summer rainfall areas, will certainly result in further support for the suggestion that macchia concurs with ecological categories 5 and 6.

Although the suggested ecological classification will probably be refined when more is known about the behaviour of the many poorly-known taxa, it has the potential of being a useful tool for preliminary comparisons of different regional faunas. Together with distribution maps, it may be possible to correlate the presence of certain taxa with the availability of suitable biomes. These correlations may be helpful in future environmental impact assessment work. The classification is broad enough to have world-wide application and so it should be possible to compare the faunas of the different zoogeographical regions once field-experienced specialists have classified the genera of these regions in terms of the suggested arrangement.

Experience has shown that many asilid species may be found living in close approximation to one another. For example, 25 species in 14 genera were recorded over a period of a few hours of one day from a single site on the Renoster River near Sutherland in the Cape Province. Although resource-partitioning appears to be responsible for this situation, a great deal of additional work needs to be undertaken before the interactions between species can be better understood. Use of the proposed system of classification would be useful, although it would probably need to be refined to allow for adequate habitat characterisation of each of the species involved.

A related question which still requires answering is 'to what degree is habitat partitioning protective'? In other words, are some Asilidae serious predators of other Asilidae, and if so, has habitat-partitioning developed as a consequence? As my asilid prey database indicates that Asilidae are the fourth most commonly preyed upon family of insects (Londt 1993), it is likely that habitat-partitioning may well be related to interspecific predation.

Nothing is known about the specific developmental requirements of the vast majority of asilid species. As the predacious larvae of all 25 Renoster River species mentioned above almost certainly live in sand or soil, it would be interesting to know something about the possible resource-partitioning which must exist subterraneously. It would also be instructive to know to what extent the larval habitat determines the habitat of the adult flies.

It is hoped that publication of this contribution towards a better understanding of the insect group which has occupied so much of my research time, will encourage other field-experienced taxonomists to attempt to record their observations. The type of information reported in this paper can only be assembled by researchers with an intimate knowledge of the taxa they encounter in the field. Therefore, contrary to general belief, taxonomists are probably the best people to promote interest in the much-needed ecological work still to be undertaken on the vast majority of insect taxa.

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